A CRITICAL SURVEY OF THE SENSE OF HEARING IN FISHES.

By G. H. PARKER.

It was the opinion of many ancient writers that fishes could hear. Thus Aristotle in his "History of Animals," Book IV., Chapter 8, after having stated that fishes possess no evident organs of hearing, declared that nevertheless they must hear, for they flee from loud noises such as those made by the oars of a trireme. Aristotle added further that fishermen were careful to avoid making a noise with their oars or their nets when they perceived many fishes collected together, and he concluded that it was evident from these considerations that fishes have a sense of hearing.

Among the Latins Pliny in his "Natural History," Book X., Chapter 89, stated that though fishes were without ears, yet it was quite certain that they could hear, for it was a well-known fact that in some fish-ponds, the fishes were called to their food by the clapping of hands and that in the fish-ponds of the Emperor they came each kind in response to its name. Thus, notwithstanding that these older writers sometimes confused dolphins and other cetaceans with true fishes, they had from unquestionable sources abundant evidence upon which to base their opinions.

The credit of having discovered, contrary to the belief of such authorities as Aristotle and Pliny, that fishes really possess internal ears, seems to rest with Casserius (1610). This discovery was quite in keeping with the opinion of the times as may be inferred from the conversation between Venator and Piscator in that delightful repository of ancient fish lore, "The Complete Angler." In the first edition of this classic (1653, p. 128) Walton makes Venator put the question to him "But Master, do not Trouts see us in the night?" And to this query Walton, in the guise of Piscator, replies, "Yes, and hear, and smel too, both then and in the day time." Whereupon he adds an account of an experiment by Sir Francis

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Bacon to show that sound is easily conducted through water and he concludes with the statement that this experiment "has made me crave pardon of one that I laught at, for affirming that he knew Carps come to a certain place in a Pond to be fed at the ringing of a Bel; and it shall be a rule for me to make as little noise as I can when I am a fishing, until Sir Francis Bacon be confuted, which I shall give any man leave to do." In the second edition of "The Complete Angler" (1655, p. 175) Piscator, who seems to have pondered the matter of fish hearing in the two years since the first edition appeared, added the following final touch. "All the further use that I shall make of this, shall be to advise Anglers to be patient, and forbear swearing, lest they be heard, and catch no fish."

In the eighteenth century the ears of fishes were studied by such workers as Klein (1740), Geoffroy (1780), Hunter (1782), Monro (1785) and others. Hunter (1782, p. 383), in commenting on the function of the ears of fishes, makes the following statement:

Thus Hunter confirmed the opinion of previous investigators, who were further supported by what was learned of the structure of the fish ear by a host of later workers including such men as Comparetti (1789), Cuvier (1805), E. H. Weber (1820) and especially G. Retzius (1881), whose monumental work on the ears of vertebrates may be said to have completed a chapter in our knowledge of this sense organ.

Retzius (1881) has reported very fully on the structure of the

"As it is evident that fish possess the organ of hearing, it becomes unnecessary to make or relate any experiment made with live fish which only tends to prove this fact; but I will mention one experiment, to shew that sounds affect them much, and is one of their guards, as it is in other animals. In the year 1762, when I was in Portugal, I observed in a nobleman's garden, near Lisbon, a small fish-pond, full of different kinds of fish. Its bottom was level with the ground, and was made by forming a bank all round. There was a shrubbery close to it. Whilst I was laying on the bank, observing the fish swimming about, I desired a gentleman, who was with me, to take a loaded gun, and go behind the shrubs and fire it. The reason for going behind the shrubs was, that there might not be the least reflection of light. The instant the report was made, the fish appeared to be all of one mind, for they vanished instantaneously into the mud at the bottom, raising as it were a cloud of mud. In about five minutes after they began to appear, till the whole came forth again."

ears of no fewer than forty-eight species of fishes. The completely differentiated internal ear of one of the higher fishes consists of a utriculus (Fig. 1, *u*) with its three semicircular canals and a sacculus (*sc*) with its appended lagena (*lg*). The utriculus is ordinarily

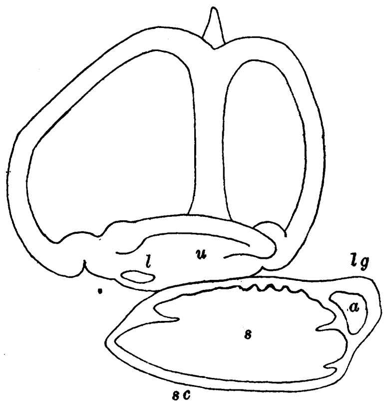

FIG. 1.

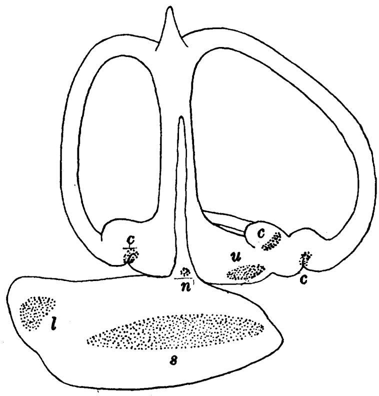

FIG. 2.

FIG. 1. Left Ear of the European Perch, *Perca fluviatilis,* lateral view, showing the three otoliths; *a,* asteriscus; *l,* lapillus; *lg,* lagena; *s,* sagitta; *sc,* sacculus; *u,* utriculus. After Retzius.

FIG. 2. Left Ear of the European Perch, *Perca fluviatilis,* median view, showing the sensory patches; *c,* crista acustica; *l,* lapilla acustica lagenæ; *n,* macula acustica neglecta; *s,* macula acustica sacculi; *u,* macula acustica utriculi. After Retzius.

connected with the sacculus by the utriculo-saccular canal. The sense organs in this type of ear reach a maximum number of seven: a crista acustica in the ampulla of each of the three semicircular canals (Fig. 2, *c*), a macula acustica (*u*) in the utriculus and a second one (*s*) in the sacculus, a macula acustica neglecta (*n*) in the utriculus, and a papilla acustica (*l*) in the lagena. No fish is known to possess a papilla acustica basilaris cochleæ or organ of Corti, which makes its first appearance in certain amphibians and is found in all higher vertebrates. Three otoliths are commonly present in the ears of the higher fishes: a large one, the sagitta (Fig. 1, *s*), on the macula acustica in the sacculus, a smaller one, the asteriscus (*a*), in the lagena, and a still smaller one, the lapillus (*l*), on the macula acustica in the utriculus.

Some fishes show considerable divergence from the plan of structure just laid down. Aside from amphioxus, which possesses no ears at all, the cyclostomes exhibit the simplest and probably the most primitive type of this sense organ. In these fishes each ear consists of a single sac with never more than two semicircular canals corresponding very probably to the anterior and the posterior vertical canals of the higher vertebrates. There are three sense organs, a crista acustica for each of the two canals and a macula acustica communis on the wall of the sac. In all higher fishes each ear-sac is double, as already described, consisting of a sacculus and a utriculus with its three semicircular canals. This type of ear possesses ordinarily the seven sense organs already enumerated, the macula acustica neglecta being, however, occasionally absent. In the elasmobranchs the utriculus and sacculus of a given ear communicate freely with each other through a relatively large opening. In the teleosts and other higher fishes a narrow tube, the utriculo-saccular canal, may connect these two parts, or they may be quite disconnected and separate. Of the thirty-three species of teleosts reported on by Retzius, eleven possessed a well-developed utriculo-saccular canal, two showed traces of it, and twenty were without the least sign of it, though in embryonic stages they presumably possessed it. These are the chief facts in the comparative anatomy of the ears of fishes. As the terminology shows, these organs were regarded as organs of hearing and this opinion was the prevailing one among scholars of the last century. It has been more or less tacitly assumed in the more important text-books of that period such as Owen (1866), Wiedersheim (1883), Gegenbaur (1898), and others.

The first noteworthy opposition to this opinion came from de Cyon (1878). This investigator, in his study of the function of the semicircular canals in vertebrates, made the observation (p. 93) that lampreys did not respond to sounds and that after their internal ears had been removed, in itself a relatively simple operation, they exhibited great disturbances in locomotion. These disturbances were to be observed seven weeks after the operation and were presumably permanent. De Cyon, therefore, concluded that the ears in this primitive fish were concerned with responses to spacial relations and had nothing to do with hearing. This opinion was supported

by the fact that the ear of this fish was unprovided with a cochlea, that organ which is present in the ears of the higher vertebrates and is especially concerned with hearing.

Some seventeen years later and apparently without knowledge of de Cyon's results, Kreidl (1895) undertook the study of the function of the fish ear. His work was carried out on the goldfish (*Carassius auratus*) and with much care and many precautions. Normal fishes in a carefully guarded aquarium were found not to respond to sounds produced in the air, or even in the water itself, though the creatures did react to a blow on the cover of the aquarium. Fishes poisoned slightly with strychnine were more sensitive and, though they did not respond to a bell or whistle sounded in the air nor to a metallic rod made to vibrate in the water, they did respond to the tapping of the rod, to the clapping of hands, and to the report of a pistol. After the removal of the ears, the equilibrium of these fishes was greatly disturbed, as was to be expected from the previous work of Loeb (1891*a*, 1891*b*), Lee (1892, 1893, 1894) Kreidl (1892), and Bethe (1894, 1899), but the animals showed no change in their responses to sounds. Kreidl (1895, p. 464), therefore, concluded that it could not be shown that the goldfish hears and that the responses that this fish exhibits to sound-waves were dependent upon a specially developed skin-sense.

The year following, Kreidl (1896) carried out some simple but conclusive experiments at Krems where large numbers of trout and other fish were bred for market purposes and where the fish were said to come for food at the sound of a bell. Kreidl showed that when the bell was rung by an unseen person, the fishes failed to assemble and that the real stimuli that caused them to come together was the sight of the keeper and the vibration of his tread. Thus Kreidl was confirmed in his view that fishes, including both goldfishes and trout, do not hear.

Kreidl's papers were soon followed by one from Lee (1898), who tested a number of species of fishes by subjecting them to the sounds of the human voice, the clapping of hands, and the striking of stones both above and under water. Though the fishes tested proved to be very sensitive to the jarring of the tank in which they were and to concussions on its walls, they did not respond to sounds produced

as already described and Lee (1898, p. 138) concluded that fishes do not possess the power of hearing, in the sense in which that term is ordinarily used, and that the sole function of their ears is equilibrium.

These conclusions were not supported by the work of Parker 1903*a*, 1903*b*) on *Fundulus heteroclitus*. Recognizing the possibility that sound might stimulate not only the skin and the ear but also the organs of the lateral-line system, three sets of *Fundulus* were tested. One set was entirely normal. A second set was prepared by cutting the roots of the fifth and seventh nerves, the lateral-line nerves, and the spinal cord a short distance behind the skull, thus rendering inoperative the lateral-line organs and the organs of touch on the whole surface of the fish except in the region immediately about the pectoral fins. In this set the ears were left intact. In the third and last set the eighth nerves were cut, thus eliminating the ears, while the receptivity of the skin was not interfered with.

These three sets of fishes were subjected to sound stimulation in a large aquarium. The sound was generated by plucking a bass-viol string attached to the wooden end of the aquarium and so arranged that its vibrations were transmitted directly through the wood to the water of the aquarium The normal fishes responded by pectoral-fin movements in 96 per cent. of the trials. The fishes in which the skin had been rendered insensitive, though greatly reduced in their powers of locomotion by the operations they had undergone, nevertheless responded in 94 per cent. of the trials. Finally the fishes in which the ears had been eliminated responded in only 18 per cent. of the trials. It was, therefore, concluded that sounds called forth responses in *Fundulus* by stimulating not only the skin but also the ears, in other words, that this fish hears. To remove any doubt as to the nature of the stimulus, an electrically driven tuning-fork of the rate of 128 complete vibrations per second was made to replace the bass-viol string on the wooden end of the aquarium. When the fork was in vibration, its base could be brought in contact with the wall of the aquarium and withdrawn at will. If this operation was carried out with a motionless fork, no response from the fishes was to be observed, but when the fork was

in vibration normal fishes and fishes in which the skin was insensitive responded quite regularly with fin movements whereas those in which the ears had been eliminated showed no reactions. Hence there seemed to be no doubt that the ear of *Fundulus* was stimulated by tones.

In view of the discrepancy between the results of Kreidl and those of Parker, Bigelow (1904) was led to retest the goldfish. Three sets of fishes were prepared corresponding to those that had been used in *Fundulus* by Parker. These sets were subjected to the tones from an electrically driven tuning-fork led into the water in which the fish was by bringing the base of the fork into contact with the wooden side of the aquarium. Normal fishes responded in 78 per cent. of the trials. Fishes with insensitive skins but normal ears reacted in 80 per cent. of the trials. While fishes in which the eighth nerves had been cut gave no responses whatsoever to the tone of the fork. These results agreed in the main with what had been obtained by Parker in *Fundulus,* but disagreed with Kreidl's results on the goldfish. Bigelow, therefore, sought for the grounds of this disagreement. For this purpose he repeated exactly Kreidl's procedure in preparing the fishes and instead of eliminating the ear by cutting the eighth nerve, he removed this organ by opening the skull and withdrawing the semicircular canals and the attached parts of the ear as Kreidl had done. On testing such goldfishes, they were found, as Kreidl had asserted, to respond to tones as normal fishes do, but on dissecting them, it was discovered that by this method only the utriculus had been taken out with the semicircular canals and that the sacculus, uninjured and intact, had been left behind. It was, therefore, clear that Kreidl's operation removed only part of the ear and that the portion left behind was the very part most likely to be concerned with hearing. Thus the discrepancy between Kreidl's work and that of Parker and of Bigelow was cleared away.

Following these results came a series of papers that were in part favorable to the opinion that fishes could hear and in part opposed to this view. Of those in opposition the first was by Körner (1905). This author tested twenty-five kinds of fishes that had become

accustomed to life in aquaria.[1] The source of sound was a "cri-cri," a child's toy consisting of a slightly deformed metal key which on being depressed gave forth a momentary high-pitched, penetrating sound. This sound was made under water at a distance of 30 to 60 centimeters from the fish and was in no instance followed by a response. Körner (1905, p. 126), therefore, concluded that hearing was an unproved function for the ears of fishes.

Marage (1906) was also unable to get any responses from seven species of fishes subjected to synthetic vowel sounds led into the water through a rubber tube closed by a thin rubber diaphragm. Six of these fishes (*Gobio fluviatilis, Anguilla vulgaris, Esox lucius, Tinca vulgaris, Cyprinus carpio,* and *Leuciscus rutilus*) were tested in confined water and one (*Alburnus lucidus*) in the open.

Brüning (1906) noted that stickelbacks in an aquarium were not disturbed by the clapping of hands even when this was done close to the top of the water and that fishes in a pond did not respond to a cry though they were startled by the tread of the observer on the bank.

Maier (1909) installed under water in an aquarium an electric bell so wired that it could be controlled from outside. With this device he tested eleven species of marine fishes (*Gadus morrhua, Clupea harengus, Ammodytes lanceolatus, Trigla gunardus, Cottus scorpius, Rhombus maximus, Solea vulgaris, Pleuronectes platessa, P. flesus, P. limanda,* and *Raja clavata*) and twelve species of fresh-water fishes (*Cyprinus carpio, Alburnus lucidus, A. bipunctatus, Idus melanotus, Gobio fluviatilis, Barbus fluviatilis, Rhodeus amarus, Anguilla vulgaris, Macropodius* sp., *Anabas* sp., *Osphromenus* sp., and *Girardinus* sp.). To the sound of the bell no reaction of any kind was given by any of these fishes and Maier (1909, p. 394) concluded that they possessed no powers of hearing. Nevertheless he was surprised to find in connection with another line of experi-

[1] The fishes tested by Körner (1905, p. 123) were as follows: *Abramis blicca, Cobitis fossilis, Gasterosteus pungitius, Idus melanotus, Petromyzon fluviatilis, Rhodeus amarus, Betta pugnax, Callichthys fasciatus, Carassius auratus,* and two varieties, *Chromis multicolor, C. tristramus, Eleotris* sp., *Gambusia affinis, Geophagus brasiliensis, Girardinus candimaculatus, Haplochilus panchax, Heros fascetus, Pœcilia mexicana, Polyacanthus viridi-auratus, Saccobranchus fossilis, Tetragonopterus* sp., *Trichogaster fasciatus,* and *T. lalius.*

mentation that the American catfish, *Amiurus nebulosus,* regularly took fright when he whistled. On testing this fish further Maier was completely convinced that it responded to sounds. It was, however, the only fish of those examined by him that so responded.

Bernoulli (1910) tested fresh-water fishes in their natural surroundings with the sounds given out by a submerged electric bell and with shrill whistling. Three species (*Salmo fario, Anguilla vulgaris,* and *Lucioperca sandra*) were subjected to the sound from the bell and two (*Salmo fario* and *Thymallus vulgaris*) to whistling. In no instance was there a response.

Haempel (1911) also used the sound from a submerged electric bell and a shrill whistle as stimuli for fishes. Five species of fresh-water fishes were tested (*Cyprinus carpio, Scardinius erythrophthalmus, Gobio fluviatilis, Trutta fario,* and the Zwergwelse = *Amiurus*). None of these fishes reacted to the sounds used except *Amiurus* which regularly responded to both the sound of the bell and to whistling. On removing the ears from a specimen of *Amiurus* and allowing the wounds to heal, the animal lost all response to the sounds employed. Haempel (1911, p. 325), therefore, concluded that while members of the Salmonidæ and Cyprinidæ cannot be said to hear, the Siluridæ and particularly *Amiurus* must be admitted to possess powers of hearing.

In consequence of the results of Maier (1909) and of Haempel (1911) Körner (1916) was led to investigate hearing in *Amiurus.* This fish was subjected to various kinds of shrill whistling, including that from an automobile whistle; to a series of musical tones, to the notes of a scale sung by the human voice, and to the sounds from a "cri-cri." To none of these stimuli was there the slightest response. Körner (1916, p. 263) was unable to explain his negative results with *Amiurus* as compared with the positive outcome of the tests made on the same fish by Maier (1909) and by Haempel (1911).

The papers that have thus far been summarized support in general the conclusion that most fishes do not hear. Those that follow have yielded evidence of an opposite kind. Piper (1906*a,* 1906*b*) prepared the ear and the eighth nerve of the pike and of

the eel so that he could demonstrate a demarcation current on these parts. On producing sounds in the water in which the preparations were, an action current was identifiable that lasted as long as the sound did. Such a current was also produced by tapping the walls of the containing vessel, but it did not result from a noiseless jarring of the preparation, nor from a stirring of the water around the preparation. From these results Piper (1906*a*, p. 296) concluded that fishes responded to sounds by means of their ears.

Parker (1909, 1911*a*) attempted to ascertain if there was any evidence for hearing in the dogfish, *Mustelus canis*, which, as previous study (1903*a*, p. 62) had shown, was not responsive to ordinary sound vibrations in water. It was found, however, that if the wooden wall of a tank containing a dogfish was struck by a heavy swinging pendulum, the dogfish within would respond by a sudden jump forward or at least by a waving of the posterior edges of the pectoral fins. The pendulum consisted of a bob weighing 3,800 grams and a suspending wire, the whole apparatus having a length of 260 centimeters. This device was calibrated so as to strike the wall of the tank with a momentum of 83,600 centimeter-gram-second units or more. The minimum stroke was taken as unity and strokes of greater magnitude could be conveniently delivered up to about five times that of the assumed unit. Normal fishes when swimming freely in the water occasionally responded by pectoral-fin movement to a stroke of magnitude 1 and invariably to a stroke of 1.5. After their eighth nerves had been cut, they did not respond to a stroke of less than 3 and invariably only to one of 4. To ascertain if this reduction in sensitivity was due to the operation they had suffered, a second set, in which for other purposes the optic nerves had been cut, were tested with the pendulum. These fishes responded regularly to a stroke of magnitude 2. To eliminate the skin and lateral-line organs, the fifth, seventh, and lateral-line nerves were cut, the spinal cord destroyed up to the neck region and the skin around the pectoral fin cocainized. Notwithstanding the extent of their preparations, these fishes responded by movements of the pectoral fins to strokes of the pendulum of magnitude 1 to 1.5. Without question their ears were receptive for these vibrations. Parker, therefore,

concluded that though dogfishes are not responsive to ordinary musical tones, they do possess hearing.

Tests carried out by Parker (1910*a*) on *Ammocœtes* by the same means as those used with the dogfish yielded similar results. This fish is sensitive to sound not only through the skin but also through the ears.

Parker (1910*b*) also studied the ears of *Cynoscion*. In this fish, as in many other acanthopterygians, the sacculus and the utriculus are entirely separate structures, there being no utriculo-saccular canal. *Cynoscion*, after having been in a large wooden tank for some time, became adjusted to its new environment and when the side of the tank was tapped vigorously, it responded by a slight forward spring. The utriculus and semicircular canals were then destroyed through a small incision on the top of the head, leaving the sacculus intact. Such fishes showed at once disturbed equilibrium, after which they recovered their upright position. On having blinders put over their eyes, however, they swam with great irregularity. Thus both eye and ear are involved in their responses for equilibrium. During all these tests, however, they reacted as normal fishes do to taps on the wall of the tank, showing that the destruction of the utriculus and semicircular canals had not interfered with their responses to sounds. It was found impossible to reverse the operation just described and destroy the sacculus leaving the utriculus intact. But by forcing a strong pin through the paper-thin bone between the roof of the mouth and the sacculus, it was possible to fix the large otolith of the sacculus, the sagitta, firmly against the outer or non-nervous wall of the sacculus and thus prevent its independent motion. Fishes treated in this way were only occasionally responsive to taps on the wooden wall of the tank. If a normal fish and one with the sagittæ pinned down were tested in the same tank, the greater responsiveness of the normal individual was easily noticed. Although the experiments on *Cynoscion* leave open the question of the extent to which the skin may participate in sound reception, they show very clearly that the sacculus of the ear, as contrasted with the utriculus, has a well-defined part in this activity.

Meyer (1910), whose work was chiefly concerned with the capac-

ity of fishes to associate, showed that goldfishes could be taught to go for food to one or another part of an aquarium depending on the sounding of a high- or a low-pitched bell, a result favorable rather than otherwise to the opinion that goldfish hear.

Without knowledge of the work of Haempel (1911) and of Körner (1916) Parker and Van Heusen (1917) undertook the study of the responses of *Amiurus* to sound and other mechanical stimuli. They were influenced in this by the hardiness of *Amiurus* and by the observation of Maier (1909) that this fish responded to a whistle. As in Parker's former experiments, attempts were made to eliminate the ears, the lateral-line organs, and the skin. In two of these operations new methods were devised. In excluding the ear nothing better was found than cutting the eighth nerve. After the operation the necessary incisions on the head quickly healed and the fishes lived well. Following the tests, fishes that had been thus operated upon were dissected to ascertain that the eighth nerves had actually been cut, an almost invariable result. In the elimination of the lateral-line organs those of the trunk were rendered inoperative by cutting the lateral-line nerves near the gill clefts and those of the head by destroying individually the forty-eight organs of that region. This was done by means of an electric depilating needle. Histological examinations of the spots thus treated showed in the preliminary tests the complete destruction of these organs. Finally, the skin was rendered non-receptive by painting it with a 20 per cent. solution of magnesium sulphate, which was allowed to act for five minutes. The skin of a fish so treated remained insensitive to mechanical stimulation for an hour to an hour and a half.

In preparing fishes for experimental tests they were always previously blindfolded by having a pair of thin leather goggle-shaped shields placed over the eyes and held there by a few stitches taken in the skin. Because of its gregarious habits *Amiurus* was always tested in pairs, single fishes being much less satisfactory for experimental work than two. In accordance with the states of their sense organs eight groups of fishes were used: first, normal fishes with skin, lateral-line organs, and ears intact; second, fishes with skin and ears intact but lateral-line organs eliminated; third,

fishes with skin and lateral-line organs intact but ears eliminated; fourth, fishes with only skin intact; fifth, fishes with only lateral-line organs and ears intact; sixth, fishes with only ears intact; seventh, fishes with only lateral-line organs intact; and eighth and last, fishes with none of the three sets of sense organs intact.

The fishes were tested in an aquarium of glass and stone, measuring 75 cm. by 35 cm. by 40 cm. This was supported on an inflated bicycle tire that rested on a table each leg of which pressed on a mass of excelsior wood chippings spread on a tile which in turn had under it a pad of rubber 1.8 cm. thick. The whole apparatus was set up on the concrete floor of a basement room in the laboratory and proved to be remarkably free from extraneous vibrations.

Of the several kinds of sounds to which the fishes were subjected, that from a watchman's whistle[2] blown vigorously in the air gave most striking results. Of the four classes of fishes in which the ears were intact all responded with clearness and certainty by swimming at once from the upper surface of the water into deeper positions in the aquarium. Those in which the eighth nerve had been cut did not respond at all to the whistle, though they responded to other stimuli, such as currents of water, water dropped on the surface of that in the aquarium, and pendulum strokes on the wall of the aquarium. Incidentally it may be mentioned that the currents of water and the drops of water proved to be stimuli for the skin only, but that the strokes of the pendulum affected not only the skin but also the ear (compare Table I., Parker and Van Heusen, 1917, p. 472).

Another means of stimulating *Amiurus* consisted in a series of tones from a telephone submerged in the water of the aquarium. This telephone was enveloped in a tightly stretched thin rubber bag. By means of a piece of apparatus consisting of a series of seven alternating-current generators with their armatures on a common shaft driven by a ten-horse-power electric motor, currents of 43, 86, 172, 344, 688, 1,376, and 2,752 cycles per second were produced. By appropriate switches any one of these could be thrown into the

[2] The sound produced by this whistle consisted of at least two elements: a low vibration probably due to the rapid oscillation of the small ball contained in the whistle, and a shrill piping note.

telephone which then yielded a tone of corresponding pitch. These tones were of a musical quality and were accompanied by harmonics. Thus the fishes in the aquarium could be subjected to any one of the seven tones from 43 to 2,752 vibrations per second without the least mechanical jar or disturbance. To be perfectly sure that the operation of the telephone had no effect upon the fishes, except through the sound it produced, its vibrating plate was removed, after which it was operated in the aquarium as in the ordinary tests. Under these circumstances no responses of any kind were obtained from the fishes. The electromagnetic field and such other incidental disturbances necessarily introduced by the telephone were thus shown to be ineffective as stimuli.

The reactions of *Amiurus* to the tones from the telephone are given in the following table:

TABLE I.

RESPONSES OF *Amiurus* TO TONES AT OCTAVE INTERVALS FROM 43 TO 2,752 COMPLETE VIBRATIONS PER SECOND.

Each number represents the number of responses in ten trials, five on each of two fishes.

Conditions of the Fishes.	Pitch of Tones in Complete Vibrations per Second.						
	43.	86.	172.	344.	688.	1,376.	2,752.
1. Normal: skin, lateral-line organs and ears functional..	10	9	7	6	4	0	0
2. Ears functional; skin and lateral-line organs eliminated	10	8	7	4	1	0	0
3. Skin functional; ears and lateral-line organs eliminated	6	4	3	0	0	0	0
4. Skin, lateral-line organs and ears eliminated.........	0	0	0	0	0	0	0

From the observations recorded in this table Parker and Van Heusen (1917, p. 477) concluded that *Amiurus* is more generally stimulated by tones of low pitch than by those higher in the scale, that both the ears and the skin are effective as receptors for these tones, but that the ears have a wider range than the skin. These results completely confirm Haempel's conclusion that *Amiurus* can hear.

The judgments that from time to time have been passed in these two lines of evidence have been almost as diverse as the evidence

itself seems to be and much has naturally depended upon the momentary phase of the subject. Lang (1903), after an extended account of the relations of the otocysts of invertebrates and the ears of vertebrates to equilibrium, concluded on the basis of Kreidl's experiments that there is no great likelihood that fishes hear, but that experiments should be tried on fishes that have differentiated structures for the production of sounds. Blochmann (1903, p. XCVI.) on similar grounds also doubted if fishes could hear. Hensen (1904) reviewed the work of Zenneck (1903) and of Parker (1903*a*) and concluded from their results that fishes do hear, a conclusion that was justly criticized by Bezold (1904, p. 159), who pointed out that Zenneck's results might be explained on the assumption that the skin was stimulated. Somewhat later Zacharias (1906) in a popular article concluded on the basis of the work of Kreidl and of Körner that fishes could not hear and misstated (1906, p. 373) entirely the results of Zenneck and of Bigelow which he claimed supported this conclusion. Two years later Körner (1908) declared that conclusive experimental evidence to show that fishes hear had not yet been produced, but he felt that it was not impossible that they possessed a certain degree of audition. In the same year Edinger (1908) pointed out the relation of sensory reactions to central nervous structures and stated on the basis of Piper's work that with fishes it was rather a question of what did they hear than did they hear. Willem (1913, p. 1247), on the basis of the evidence already cited, argued in favor of hearing. Watson (1914, p. 393), after reviewing the more important statements pro and con on the question of fish hearing, summed the matter up in the sentence: "It seems very difficult to reach any conclusion in the face of such contradictory evidence."

In attempting to sift what has been thus far advanced on the problem of fish hearing, it is natural to begin with the query of what would constitute hearing in a fish. Both Kreidl (1895) and Lee (1898) have discussed this question in the light of their own experiments. Kreidl (1895, p. 461) has pointed out that it is not in accord with ordinary usage to speak of hearing as any sensory disturbance produced in an animal by a vibration propagated through

the surrounding medium. Such disturbances, as has long been known, may stimulate the organs of touch as well as the ear. Kreidl, therefore, rightly maintained that these disturbances must be shown to stimulate the ear before they can be said to be stimuli for hearing. Lee (1898, p. 138) has also emphasized the importance of regarding hearing "in the sense in which the term is ordinarily used." It seems, therefore, fair to conclude that any disturbance that can be said to produce hearing through the human ear may also be said to call forth hearing in a fish provided it can be shown to act through the ear and not simply through the skin or other such receptive surface.

The human ear is normally stimulated by a great variety of sounds, some in the nature of tones and others in the nature of noises. We hear not only the tones of a tuning-fork, but the less pure tones of musical instruments, and of the voice as well as an immense array of very irregular disturbances, difficult to describe from a physical standpoint and classed generally as noises. Perhaps among the most extreme of these are explosive noises such as are produced by the clapping of hands, the discharge of firearms and so forth. All of these we certainly hear, for they affect us chiefly through the ear and their inefficiency as stimuli for the deaf is well known.

When they are extreme, they produce what we commonly speak of as shock or concussion and there has been a tendency on the part of some workers (Bateson, 1890, p. 252) to regard the shock as distinct from the sound. From a physical standpoint there seems to be no grounds for this assured distinction. The powerful disturbance that emanates from the midst of an explosion is not made up of sound and shock or concussion, but is a single complex disturbance which when it strikes our bodies may stimulate ears, skin, and even other sense organs. In so far as it affects our ears, however, we must admit it as a stimulus for hearing. Kreidl (1895, p. 459) has pointed out that sounds with shock quality are more effective as stimuli for fishes than ordinary tones are, and the experimental work of later investigators goes far to substantiate this conclusion. Nevertheless, for reasons already given, this state of

affairs does not militate against the use of this class of sounds as stimuli for the ear. It is, therefore, entirely appropriate to use such sounds in testing hearing in fishes, but the experimenter must show beyond a doubt that they do stimulate the ear, otherwise evidence derived from such tests fails to touch the problem. The test for hearing in fishes is the proved presence of a response mediated by the ear and dependent upon some vibratory physical disturbance in the water which disturbance may vary from the extreme regularity of a pure tone to the extreme irregularity of a noise such as the report of a gun or other like explosion.

In discussing hearing in fishes, Lang (1903, pp. 44, 48) expressed the opinion that these animals probably possess through the ear a sense of trembling (Erschütterung, Erzitterung) rather than one of true hearing and that this sense of trembling is a forerunner of hearing. In distinguishing the sense of trembling from that of hearing he states that in the former the pressure waves are perceived as a series of more or less distinct and separate entities, whereas in hearing the impression is more homogeneous. This distinction is one that pertains to sensation and, therefore, it can hardly be made the basis of experimental tests in fishes. It, moreover, implies that we cannot be said to hear sound vibrations whose note is so low that the single beats fail to fuse. But that we hear these beats as well as we do tones is beyond dispute and Lang's distinction, therefore, is in reality without support. Something of the same view has been expressed by Bernoulli (1910, p. 639) who, however, assumes the receptor for such beats to be the skin not the ear.

Lang (1903, p. 48) and a few other workers have also intimated that hearing is a process that probably cannot be carried out in water, but is necessarily associated in some way with the air. A little thought, however, will show that this position is quite untenable, for watery fluids bathe the end organs of the internal ears of all vertebrates whether they be inhabitants of the air or of the water. If fishes hear, sounds normally reach their ears much more simply and directly than in the case of air-inhabiting forms, for such disturbances pass at once through fishes' bodies and require no

translation from an air medium to a water medium as they do in air-inhabiting vertebrates. When, therefore, as occasionally happens, a fish takes up with a temporary residence in the air, it should not be expected to be very responsive in this situation to sounds. This seems to be the case with *Periophthalmus phya,* which often deserts the water for the shore and which, when in the air, is apparently quite deaf even to the report of a shotgun (Johnstone, 1903, p. 300). It is only after the development of some form of translating apparatus, such as an ear-drum and a middle ear, that it would be fair to expect such animals to show much response to sounds in the air. Organs of this kind characterize the ears of air-inhabiting vertebrates and represent a means of overcoming an auditory obstacle which fishes have not had to meet, for, as has just been made clear, there is not the least ground for assuming that from a physical standpoint water-inhabiting animals find any impediment to hearing.

It is a well-known fact that sounds produced in the air penetrate water to only a very slight degree and, conversely, that sounds generated in the water pass out into the air only to a correspondingly limited extent. The ordinary surface between air and water is an excellent reflector of sound. Parker (1911*b,* p. 4) found that even the loud noise from a motor boat was only faintly heard by an observer who dove close to the boat and Watson (1914, p. 393), when under four feet of water, was unable to hear the report of a revolver discharged in the air overhead. It is, therefore, not surprising that *Fundulus,* though very sensitive to sounds, did not respond to the report of a saluting charge of two pounds of gun-powder exploded from a six-pound howitzer until the fish was within thirty feet of the muzzle of the gun when to the human ear the sound was deafening (Parker, 1911*b,* p. 8). These conditions were fully appreciated by Bateson (1890, p. 251) when he remarked apropos of certain tests on pollack: "As might be expected, none of the fishes were seen to take notice of sounds made in the air." Such sounds, as has already been shown, fail in large part to enter the water, being mostly reflected from its surface back into the air.

It is probably due to this circumstance, rather than that fishes do not hear, that the tests of a number of investigators who used

sounds generated in the air yielded negative results. Kreidl's (1895, p. 458) inability to stimulate goldfishes by bells and whistles may thus be explained as well as Lee's (1898, p. 137) failure to get responses to the human voice, clapping of hands, and striking together of stones. This may also have been the case with the experiments of Marage (1906), notwithstanding the care with which a translating diaphragm was used, and it seems quite certainly to have been true of Bernoulli's observations (1910, p. 643), according to which *Lucioperca* failed to respond to a pistol shot from a boat at the distance of two kilometers. When fishes in water do respond to sounds made in the air, as in the case of *Amiurus* (Maier, 1909; Haempel, 1911; Parker and Van Heusen, 1917), it must be taken as evidence of very unusual sensitiveness. As a rule such responses are not to be expected, for, as already stated, sound in the air enters water to only a very slight degree.

The production of sounds by fishes is not without its bearing on the question of fish hearing. Kreidl (1895, p. 463) appreciated this side of the problem when he argued that "Die Thatsache, dass es auch Fische gibt, die Töne hervorzubringen im Stande sind, welche möglicher Weise den Zweck haben können, as Lockmittel zu dienen, lässt immerhin die Möglichkeit zu, dass bei diesen Species bereits eine geringe Ausbildung des Gehörorganes stattgefunden hat." The importance of testing such species was emphasized by Lang (1903, p. 48). In the seventh volume of the "Cambridge Natural History," Bridge (1904, pp. 355–365), after remarking that "contrary to popular belief sound-producing or vocal organs are by no means uncommon in fishes," gives an extended account of the various means that fishes possess for the production of sounds. In some instances the sounds produced by them are unquestionably accidental accompaniments of other types of activity, but in other cases the sounds are dependent upon such differentiated mechanisms that it is impossible to attribute these emanations to accident. One instance alone will suffice. Of the fishes studied by Parker (1903*a*, p. 48: 1910*b*) *Cynoscion* produces a deep drumming sound audible when the fish is in the air to a distance of at least fifty feet. This sound is produced only by the males (Smith, 1905, p. 377) and Tower (1908) has shown that it results from the vibratory action

of a special muscle on the abdominal organs and particularly on the air-bladder. The females not only do not drum, but they do not possess the drumming muscle. This condition of high specialization, which is doubtless connected with the breeding habits of *Cynoscion,* is common to many of the sound-producing fishes and makes it impossible to agree with *Körner* (1905, p. 103) in dismissing all such cases as of accidental nature. Though it is possible that fishes produce sounds that are in some way serviceable to them but that they themselves do not hear, it is very unlikely that such is the case and the occurrence of instances of unisexual sound production, as in *Cynoscion,* strongly suggests the presence of the sense of hearing rather than the reverse.

It is reasonable to suppose that if fishes hear, they will show some form of response to sounds. If it could be demonstrated that no fish responds to sounds of any kinds, it would be highly improbably that fishes heard. Several investigators have thus tested fishes and, without reference to skin or ear, they have attempted to ascertain whether in fact fishes respond to sounds at all. Such investigations are fundamentally important for the problem at hand but, as already explained, they do not allow of a discrimination between touch and hearing. Bateson (1890, p. 251) noticed that to the vibrations from blasting pouting scattered, sole, plaice, and turbots buried themselves, and congers drew back a few inches. To a blow on the aquarium wall pollack made an obvious response. Kreidl (1896, p. 585) stated that *Salmo iridens* was stimulated by the vibration from the human footfall. Zenneck (1903) found that *Leuciscus rutilus, L. dobula,* and *Alburnus lucidus* swam away from an electrically driven bell immersed in a stream. Parker (1903*a,* p. 62) showed that mackerel (*Scomber scombrus*) and menhaden (*Brevoortia tyrannus*) responded to the vibration of a cord applied to an aquarium. Lafite-Dupont (1907) found that, except for two elasmobranchs (la Roussette, la Torpille), the other fishes tested (le Grondin papillon, la Vieille, le Mulet, la Sole) were responsive to a stroke on the side of the containing vessel. Parker (1912) found that certain fishes, *Tautoga, Stenotomus, Menticirrhus* and *Spheroides,* avoided the end of an aquarium at which blows were delivered by a swinging pendulum, that *Prionotus* gathered near this

source of sound, and that *Fundulus*, though much disturbed by the sound, tended to go neither toward the source nor away from it. These positive results show that many fishes respond to noises or even tones, but they do not throw light on the question of the particular sense organ concerned and consequently it cannot be stated whether they are due to stimulation of the ears or of the integumentary sense organs or of both.

As opposed to this line of evidence several investigators have reported lists of fishes that are said not to respond to sounds in any way. As already noted in an earlier part of this paper, Körner (1905) recorded twenty-five kinds of fishes none of which responded to the sounds from a "cri-cri." This is certainly a formidable list. When Körner learned through the work of Maier (1909, p. 394) and of Haempel (1911, p. 325) that *Amiurus* reacted to a whistle blown in the air as well as to sounds from a submerged electric bell, he undertook to test this fish with a variety of whistles, the human voice, and other sound-producing devices including the "cri-cri." His results were completely negative (Körner, 1916, pp. 263, 267), and he confessed his inability to explain the conflict between this outcome and the results of Maier and of Haempel. Parker and Van Heusen (1917) have shown not only that *Amiurus* is receptive to sounds but that, in respect to this stimulus, it is an exceedingly sensitive fish. Their method of work throws some light on Körner's results. When *Amiurus* was to be tested by them for response to sound, blindfolded individuals were put into a large aquarium. Here they appeared to settle themselves quickly near the bottom and to assume in a short time a condition in which it was reasonable to carry out tests. But in this state they seldom responded to sounds and it was only after they had been some hours, or better a day or so, in the aquarium that they really arrived at a condition of responsiveness. After this period they began to desert the bottom and to swim in the upper water, and in this state they were most responsive to sound. When thus swimming near the top, a blindfolded *Amiurus* would immediately descend to the deeper water in response to a very slight finger-tap on the slate wall of the aquarium. It was only under these conditions that Parker and Van Heusen obtained responses to a whistle or to sounds from the

telephone. If the hand of the experimenter was held in the aquarium water, be it ever so carefully done, the *Amiurus* immediately descended to the deeper parts and responses to the more delicate forms of stimuli were completely inhibited. Hence Körner's method of operating a "cri-cri" by hand under water could have had no other result that that of rendering the fishes quite unresponsive and it would have been surprising if he had obtained anything but negative results. As this responsive phase of *Amiurus* seems to have entirely escaped Körner's attention, it is natural that he should also have failed to observe the reaction of this fish to whistles, and to other sound-producing devices. Hence so far as *Amiurus* is concerned Körner's negative results, as contrasted with those of Maier (1909), of Haempel (1911) and of Parker and Van Heusen (1917), are quite clearly due to defective technique and as this technique was also the basis of his tests of the twenty-five kinds of fishes first reported by him as without hearing, it follows that these tests can no longer be regarded as valid and that Körner's statements based upon them are, therefore, without weight.

Another source of error in the testing of fishes for hearing is the assumption that their only form of response to sound is flight. From the time of Aristotle this has been known to be a typical response, but that it is the only method of reaction to sounds is far from true. Kreidl (1896, p. 585) in his experiments at the fish basins in Krems got evidence that certain fishes would approach a center of vibratory disturbance and Parker (1912, p. 103) showed that *Prionotus,* which produces a loud grunting noise, approaches a sound center rather than retreats from it. Thus, though fishes under most experimental conditions commonly are put to flight by sounds, they occasionally may do the reverse and under more natural conditions this may be a much more usual form of response than has been suspected. But whether fishes approach or avoid a source of sound, their responses in such activities are chiefly through their fins. It is, therefore, not surprising that in experimental tests sound, and particularly slight sounds, call forth very characteristic fin movements. As these movements follow with such regularity on the application of this stimulus, to deny them as a sign of effective stimulation is to ignore that very feature which may be of prime

importance in the determination of an experimental result. Hence it is not surprising that Haempel's outcome on *Cyprinus, Scardinius, Gobio,* and *Trutta* should have been negative, for he states (1911, p. 320) at the outset that movements of the pectoral fins, of the caudal fin, and of the respiratory apparatus, however called forth, are not accepted by him as evidences of sound stimulation. To any one familiar with the responses of fish such a declaration must seem to say the least, arbitrary and condemns without further ado any negative results that its author might claim. Such movements are often most characteristic and significant and they call for close scrutiny and careful observations. Although they can be seen clearly and beyond question when the fishes are in aquaria, they would very probably escape attention when these creatures are at some distance in open water. In consequence it seems doubtful if negative results recorded under these conditions (Bernoulli, 1910, p. 640) can be said to be well grounded.

From the observations of Parker and Van Heusen (1917, p. 477), it is clear that *Amiurus* is by no means equally responsive to tones of different pitches. It responded with greatest certainty to tones of 43 complete vibrations per second, and with less and less certainty to succeeding octaves up to 688. It failed entirely to respond to the two tones above 688, namely 1,376 and 2,752. It is, therefore, clear that *Amiurus* is much more receptive to tones of a low pitch than to those of a high pitch. Since most of the sounds produced by fishes are of low pitch, being described usually as croaking, grunting, or drumming sounds, it is probable that fishes are adapted chiefly to this class of tones. It is, therefore, not impossible that many tests that have yielded negative results may have done so because the tones employed were too high in pitch for the fishes. This may have been the case in the sound from the "cri-cri" employed by Körner (1905, 1916) and with that from the electric bells used by Maier (1909), by Bernoulli (1910), and by Haempel (1911). If the sounds thus produced were out of range for the fishes, it is not to be expected that they would react. All such tests, therefore, that have yielded negative results are open to this objection until doubt on this point has been removed. Thus the negative evidence of practically all the recent workers on this sub-

ject is thrown under suspicion and it, therefore, remains to discuss this problem from the standpoint of the few cases of positive evidence.

These few instances cover a considerable range of fishes. They begin with *Ammocœtes* which is apparently not responsive to ordinary noises (de Cyon, 1878, p. 93) though it will react by a winking movement of its oral hood and by curving its body when the wall of its aquarium is struck by a swinging pendulum. After cutting the eighth nerves, these responses can be called forth only by a stroke at least three times as strong as in the previous instance, thus showing that the ear is decidedly more sensitive to this stimulus than the other receptors in the body, very probably those in the skin (Parker, 1910*a*, p. 470).

Mustelus exhibits conditions very similar to those in *Ammocœtes*. It is not responsive to tones (Parker, 1903*a*, p. 62) and to ordinary noises (Lafite-Dupont, 1907), but it reacts with a sudden jump forward or a quivering of the pectoral fins to a pendulum stroke on the wall of its aquarium (Parker, 1909, 1911*a*, p. 48). On cutting the eighth nerves, three times the former stimulus was required to call forth the response previously noted. This fin-movement remained normally elicitable in fishes whose skin had been desensitized by combined nerve-cutting and treatment with cocoaine, but disappeared entirely from them on cutting their eighth nerves. Thus *Mustelus* is responsive through the ear, and less so through the skin, to the noise produced by a stroke on the wall of its aquarium.

Among teleosts three cases call for consideration: *Fundulus, Carassius* and *Amiurus*. The grounds for concluding that *Fundulus* (Parker, 1903*a*) and *Carassius* (Bigelow, 1904) hear have already been briefly stated in the earlier part of this paper. Each fish responds by at least fin-movements to the tones of a tuning-fork and to other sounds. These responses cease in part or wholly on cutting the eighth nerves. They are not greatly reduced by very extensive nerve-cutting through which much of the skin can be rendered insensitive. The responsiveness of the fishes under these conditions shows that the operation of cutting the eighth nerve cannot be regarded as the occasion of the decline in sensitivity of the particular group in which this operation was carried out but that this decline

must be ascribed to the loss of the ear as a receptor. Hence the futility of the objection that the cutting of the eighth nerve involves in itself serious inhibition. Watson (1914, p. 394) has urged against these results the criticism that the sound-producing apparatus "used by Parker and by Bigelow," an electrically driven tuning-fork, "is open to the severest kind of criticism." No further comment is made on this point and the reader is left in uncertainty of what should have been used except for the remark (p. 394) that it is strange that Parker did not repeat Bateson's experiment of tapping stones under water. Such comments as these show a very imperfect appreciation of the conditions under which tests on fish hearing can be carried out, for it is extremely doubtful if anything of value could be obtained by Bateson's procedure whereas that so severely condemned yielded position results. Hence there appears to be no good grounds to oppose the conclusion that both *Fundulus* and *Carassius* hear.

Notwithstanding Körner's negative results (1916) the unusual responsiveness of *Amiurus* as shown by Maier (1909), Haempel (1911), and Parker and Van Heusen (1917) is beyond doubt and Haempel's tests of a fish from which the ears had been removed is strongly indicative of hearing. This conclusion is abundantly confirmed by the much more extensive experiments of Parker and Van Heusen already summarized. The fact that these investigators used a submerged telephone as a source of sound and avoided much of the nerve-cutting previously employed in eliminating lateral-line organs and the skin has removed practically all of the assumed objections to the earlier work of Parker. They confirm, beyond doubt, Haempel's conclusion that *Amiurus* can hear.

The part of the fish ear concerned with hearing has not yet been determined with certainty. The condition seen in many of the higher fishes in which the two chief parts of the ear, the utriculus and the sacculus, are completely separated, suggests at once different functions for these parts. And the fact that in the goldfish the animal still responds to sounds after the removal of the utriculus and its appended canals (Bigelow, 1904) offers the natural suggestion that in this fish hearing is associated with the sacculus. This view is supported by Parker's observation (1910*b*) that when the

large otoliths in the sacculi of *Cynoscion* are pinned off against the non-nervous walls of these organs, responses to sounds largely cease, whereas a destruction of the utriculi and semicircular canals does not affect hearing. These observations support Piper's conclusions (1906*a*, 1906*b*) based on experiments involving what were without doubt the saccular otoliths. Thus, the sacculus, rather than the utriculus, seems to have to do with hearing in fishes. In this connection it is interesting to record the observations of Smith (1905, p. 378) to the effect that in those sciænid fishes that make drumming noises the otoliths from the sacculi are exceptionally large, whereas in *Menticirrhus,* a sciænid which does not drum, they are relatively small, thus suggesting a relation of the sacculus to hearing as was suspected by Scott (1906, p. 49). Without, therefore, putting too great confidence in these somewhat fragmentary observations, it seems probable that in the ears of the higher fishes where utriculus and sacculus are well differentiated, the sacculus has to do with hearing and the utriculus with equilibrium.

The bearing of this conclusion on the functional interpretation of the parts of the internal ear in the higher vertebrates must be obvious. It points at once to the macula acustica sacculi as a possible organ of hearing. Whether, in mammals, for instance, this saccular organ is concerned with hearing or not must, of course, be settled by experiment (compare Richard, 1916), but so far as the condition in fishes is concerned, it is not unreasonable to anticipate an auditory function for it. Its function, however, must be very different from that of the cochlear organ, for while the cochlea is without much doubt the organ of the ear concerned with tone discrimination, the macula acustica sacculi is probably at best only a means of distinguishing between the presence or absence of sound, including possibly its intensity. In this primitive way fishes probably hear, for it is unlikely, since they lack a cochlear organ, that they respond in any differentiated way to differences of tones. Their hearing is probably to be compared to the vision of the totally color-blind, rather than to that form of vision in which colors are discriminated.

But the fish ear is not only primitive in itself; it exhibits in its various conditions several grades of proficiency. In not a single

primitive fish, cyclostome or elasmobranch, has the ear been shown to be a receptor for what may reasonably be called tones. The ears of these lower fishes are stimulated only by relatively loud noises such as have been shown to be effective stimuli for the skin. In the higher fishes, the teleosts, the ears are not only stimulated by noises of the kind just mentioned, but they are stimulated by much less intense sounds and sounds more in the nature of tones. In this respect they mark a great advance over the condition found in the lower fishes, a condition probably phylogenetically earlier.

From this standpoint it is maintained that fishes from the cyclostomes to the teleosts have been shown to have, in varying degrees, powers of hearing. While it is easy to agree with Haempel (1911, p. 325) that *Amiurus* can hear, it is quite impossible to accept his further conclusion that "unter den Süsswasserfischen einzig und allein den Welsen die Fahigkeit des Hörens zukommt." That these fishes are the only ones that hear is so unnatural a conclusion that it carries with it its own refutation.

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